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Deepest demersal fish community in the Sea of Japan: A review

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ABSTRACT Deep sea demersal fish community in the Sea of Japan was reviewed chiefly on the basis of *Kaiyo-Maru* collections in 1970 along with other data available for the depth ranges until ca. 2000 m. From relationships of species richness with depth in relation to peculiar hydrographic conditions of the Sea, fish species found below a depth of 500 m was tentatively defined as true deep sea forms. Of a total of 20 species from 7 families of this fauna usually having eurybathic distribution, only 6 species referable to the secondary deep sea fishes inhabit the bottom deeper than 1000 m. Until a depth of 2000 m, they disappear from this community with increasing depths in the order of *Aptocyclus ventricosus*, *Bathyraja smirnovi*, *Careproctus trachysoma*, *Petroschmidtia toyamensis*, *Malacocottus gibber* and *Bothrocara hollandi*. Biological aspects of main species, particularly of *B. hollandi*, are described with special references to bathymetric series of size frequency and reproductive characters, besides several systematic annotations including the presence of two morphotypes in *B. hollandi*. In general, there are 'smaller-deeper trend' in these fauna except *M. gibber*. They also shared moderately to very low fecundity coupled with moderate to extremely egg sizes in common. Based on the stomach content analysis and feeding types, their food web interactions were outlined, suggesting a relatively well balanced community structure largely depending on the pelagic prey animals at least above a depth of 1000 m. It is concluded that so-called "taraba-community III" represents the deepest demersal fish community in this sea, whereas its fauna and structure changes remarkably with depth, finally monopolized by *B. hollandi* until at least a depth of about 2000 m.

KEY WORDS demersal fish community / the Sea of Japan / deep sea / taraba-community / eurybathic distribution

Introduction

As is well known, coastal regions of the North Western Pacific are peculiar in having a series of marginal seas comprising the Okhotsk Sea, the Sea of Japan and the Yellow Sea from north to south. This topography resulted in their characteristic zoogeography in close association with varying hydrographies (Nishimura, 1983). Of these, the Sea of Japan is marked by its highest degree of isolation: sill depths of four narrow straits connecting the Sea with the Pacific side are shallower than 140 m, while the deepest depth exceeds 3800 m.

Such a feature is responsible for its unusual hydrography, particularly of the deepwater system uniformly occupied by the so-called "Japan Sea proper water" less than 1°C. Resulting zoogeographical peculiarities were thoroughly reviewed by Nishimura (1965a–1969), in which the extremely poor fauna below a depth of 200–300 m belonging to the "taraba-community III" was considered to represent the deepest assemblages of the sea, including fish. Complete absence of the so-called ancient type deep sea demersal fishes

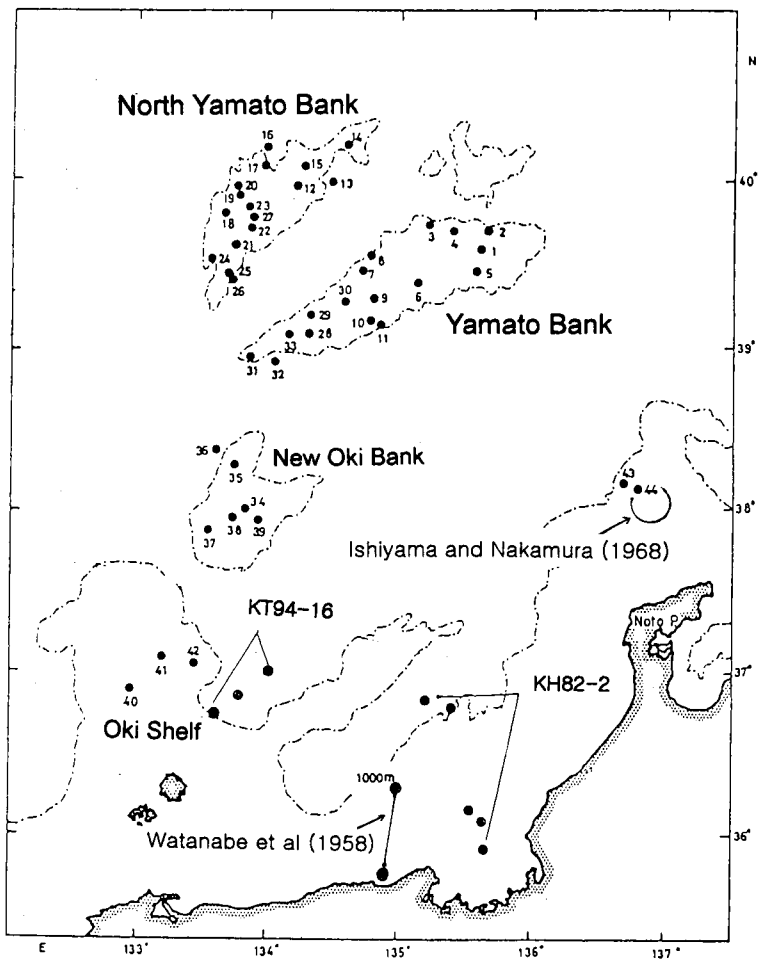

Fig. 1. Sampling localities of deep-sea demersal fishes. Numerals attached to closed circles indicate the order of trawls in *Kaiyo-Maru* cruise.

sensu Andriashev (1953) was also emphasized there. Although such features were confirmed by later studies such as Ogata et al. (1973), Okiyama (1993) and Yeh (2001), details of this community structure and its trophic biology, particularly in the deeper basin remain to be studied.

The purpose of this paper is to define again the deepest demersal fish community of the Sea of Japan, in the hope of settling following questions: "What species can be the deepest representative ?" and "How deep they can thrive there ?"

Materials and Methods

Main data sources are as follows:

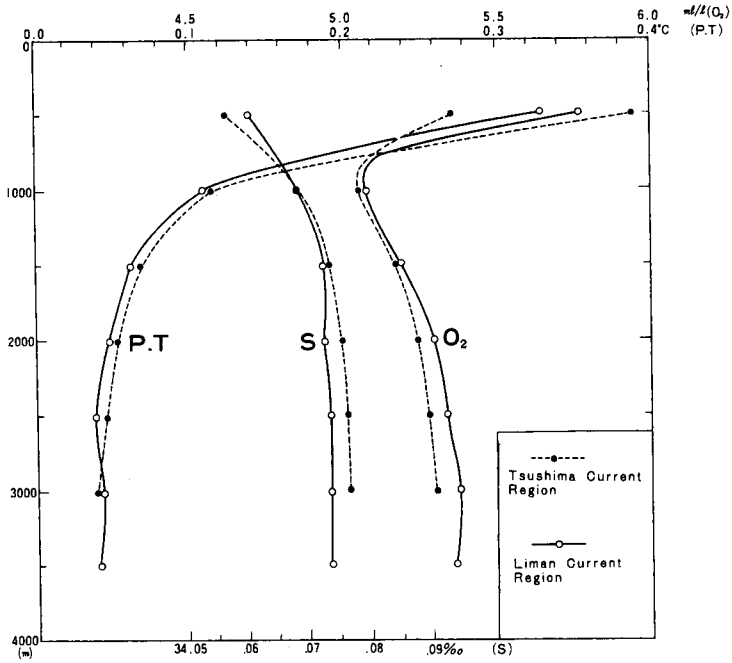

Fig. 2. Vertical distribution of mean potential temperature (P.T), salinity (S) and dissolved oxygen (O_2) in the Sea of Japan in the period of 1966–1970 (after Nitani, 1972).

(1) R/V *Kaiyou-Maru* cruise: 1970. 5.30 – 6.17; 30 minutes haul of large scale otter trawl(estimated span at otters 70 m, and at the mouth of main net 20 m), covering about 54000 m^2 in extent; 44 stations (including unsuccessful one trial) between 250 and 1220 m deep. Details of this '*Kaiyo-Maru* collections' were included in the preliminary report (Ogata et al., 1973).

(2) R/V *Hakuho-Maru* cruise (KH 82-2): 1982.4.27 – 5.26; 30 minutes tow of 3/4 m beam trawl at about 2 knots; 1043–1740 m in depth.

(3) R/V *Tansei-Maru* cruise (KY 94-16): 1994.9.22 – 9.30; 1 hour haul of 3 m beam trawl at about 2 knots; 985–1980 m in depth.

(4) Ishiyama and Nakamura (1968): T/S *Umitaka-Maru* ; July, 1968; 1 hour haul of 3 m beam trawl at about 2 knots; 390–815 m in depth.

(5) Watanabe et al. (1958): F/V *Hyogo-Maru*; October, 1956 – May, 1957; commercial trawl; seven stations with depth interval of 50 m between the depths of 100 and 400 m.

Sampling localities of these surveys are shown in Fig. 1.

Results and Discussion

1. Kinds, abundance and distribution

Vertical distribution of main hydrographic features in the Sea of Japan are shown in Fig. 2. For the summer condition, lower water system relevant to this article

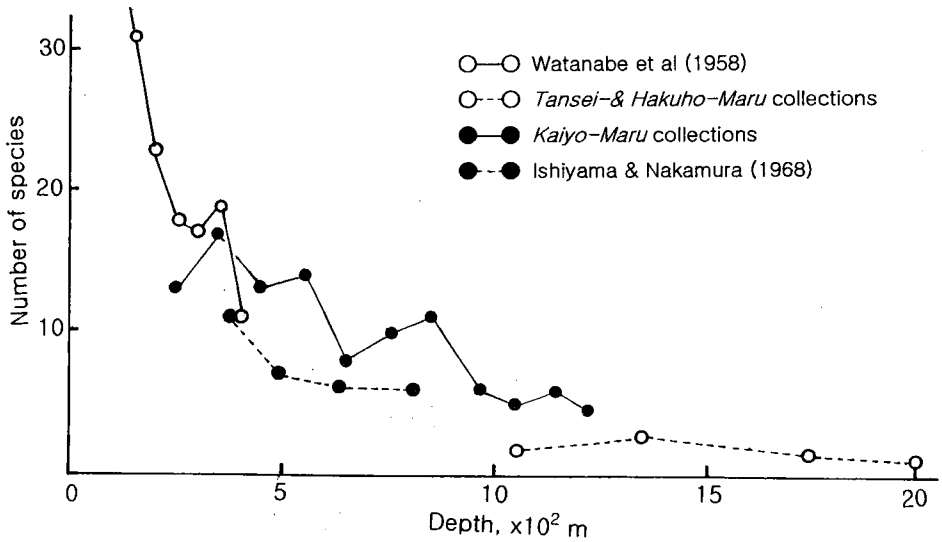

Fig. 3. Vertical profile of numbers of demersal fish species in the deep sea down to 2000 m in the Sea of Japan.

is divided into "deep water" and "bottom water": the former occupies the depth zone of ca.400 to ca. 600–800 m in the southeastern region, and the latter ca. 500–1000 m to bottom throughout the sea, respectively (Nishimura, 1967).

Numbers of demersal fish species collected by means of different kinds of bottom trawls are plotted against depths irrespective of gears (Fig. 3). Although these collections were made in the south-eastern part of the sea including offshore banks, maximum numbers of species in Fig. 3 would represent possible limit of the deep-sea demersal fish fauna of the sea considering its characteristic hydrography.

It is expected that long-term and intense survey in the sea off San'in district with the commercial trawl by Watanabe et al. (1958), might provide the best list of demersal fish fauna in the shallow zones, in which species richness decreased abruptly with increasing depths down to the upper shelf break. Similarly, huge and extensive *Kaiyo-Maru* collections show gradual decrease of species richness of much deeper fauna with its less clear decline around the depths of 300–500 m. In view of this evidence and hydrographical conditions, the upper limit of taraba-community III can be more precisely defined by shifting downward to the level of about 500 m

Deep sea demersal fish community below a depth of 500 m thus defined amount to 20 species in 7 families (Table 1). Possible addition of new forms to this community is less likely. They share eurybathial distributions from depths shallower than 300 m, but the majority of them are of occasional occurrence and only six species of abundant occurrence extend their habitats downward beyond a depth of 1000 m. Although very limited, additional deeper records beyond the reach of *Kaiyo-Maru* collections (Table 2), illustrate the probable order of extinction such as *C. trachysoma*, *P. toyamensis*, *M. gibber* and *B. hollandi*. This last species is likely to thrive even in the depth around 2000 m or more.

Table 1. Kinds, size, and abundance of deep sea demersal fishes in the Sea of Japan below a depth of 500 m.

Family Species	Depth range (m)	Abundance	Largest size (cm)	Sources**
Rajiidae				
Bathyraja smirnovi (Soldatov and Pavlenko)	100 - 1225	+++	105 ,TL	1
Gadidae				
Theragra chalcogramma (Pallas)	0 - 1225*	++	58,SL	1
Psychrolutidae				
Malacocottus gibber Sakamoto*	250 - 1740	+++	28,SL	1
Cyclopteridae				
Aptocyclus ventricosus (Pallas)*	0 - 1120*	+	37,SL	1
Liparidae				
Careproctus tracysoma Gilbert and Burke	150 - 1345	+++	35,SL	1,2,4
Careproctus colletti Gilbert	300 - 905	+	84,SL	1,
Crystallichthys matsushimae (Jordan and Snyder)	180 - 800	+		4
Liparis ochotensis Schmidt	150 - 840	+	33.5,SL	1
Zoarcidae				
Bothrocara hollandi (Jordan and Hubbs)	150 - 1980	+++	36,TL	1,2
Petroschmidtia toyamensis Katayama	200 - 1433	+++	34,TL	1,2
Lycodes nakamurai (Tanaka)	150 - 930	++		1,5
Lycodes tanakae Jordan and Thompson	150 - 870	++	84.2,TL	1
Lycodes japonicus Matsubara and Iwai	200 - 985	+	10.2,TL	1
Lycodes macrolepis Taranetz and Andriashev	225 - 560	+	25.7,TL	1,6
Lycodes matsubarai Toyoshima	310 - 590	+		3
Stichaeidae				
Lumpenella longirostris (Evermann and Goldsborough)	371 - 815	+		7
Trichodontidae				
Arctoscopus japonicus (Steindachner)	100 - 870*	++	21,SL	1
Pleuronectidae				
Hippoglossoided dubius Schmidt	200 - 720	++	34,SL	1,8
Hippoglossoides pinetorum (Jordan and Starks)	200 - 704	+	37,SL	1,9
Glyptocephalus stelleri (Schmidt)	200 - 515	+	29,SL	1
Acanthopsetta nadeshnyi Schmidt	310 - 570	+	37.5,SL	1

* Pelagic or benthopelagic occurrences are probable.

** 1, *Kaiyo-Maru* collection; 2, *Tansei-Maru* collection; 3, Nambu et al (1992); 4. Nambu and Kido (1990); 5, Nishimura (1966); 6, Katayama (1949); 7, Ishiyama and Nakamura (1968); 8, Hirose and Minami (2002); 9, Kanamaru (1996).

It is remarkable that other collections based on decidedly smaller gears gave slightly lower but similar figures of species richness with those revealed by the large gears in Watanabe et al. (1958) and *Kaiyo-Maru* collections. Such would surely imply that relevant species particularly in the deep sea system share a similar sedentary lifestyle as well as relatively uniform and abundant distributions in close association with peculiar hydrography of the sea.

These species are tentatively subdivided into three categories such as abundant,

Table 2. Number of specimens (size range in mm) of deep sea demersal fishes in *Tansei-Maru* collections below a depth of 1300 m.

Species	Depth (m)			
	1345-1365	1429-1437	1740	1980
Careproctus trachysoma	1 (120, SL)			
Petroschmidtia toyamensis		2 (102-111, TL)		
Malacocottus gibber	6 (135-183, SL)		1 (178)	
Bothrocara hollandi	5 (142-192, TL)	82 (80-200)	78 (140-220)	36 (165-197)

common and rare elements, chiefly based on the relative abundance in *Kaiyo-Maru* collections (Ogata et al., 1973) (Table 1). The abundant group comprises only four species in different families including *Careproctus trachysoma* (occurrences in 90.7 % of *Kaiyo-Maru* stations), *Malacocottus gibber* (100 %), *Bothrocara hollandi* (100 %), and *Thereagra chalcogramma* (26.5 %). Except for the last species collected in large quantities at St. 28 (365 m) on the Yamato Bank, other three occurred at all or most stations with some geographic trends like "offshore type" in *C. trachysoma*, "uniform type" in *M. gibber*, and "inshore type" in *B. hollandi* (Fig. 4).

Of the common group comprising *Bathyraja smirnovi* (95.3 %), *Petroschmidtia toyamensis* (83.7 %), *Arctoscopus japonicus* (39.5 %), *Atpocyclus ventricosus* (37 %), *Lycodes nakamurai* (27.9 %) and *Hippoglossoides dubius* (9 %), first two species were similarly widespread as in previous group, while others generally tended to have local distributions referable to either inshore or offshore types. Despite poor abundance, *A. ventricosus* had the uniform type of distribution. None of the rare group occurred in the depths below 1000 m.

Recent surveys in KT and KH cruises covering depths beyond *Kaiyo-Maru* collections did not produce any new forms, so that it can be safely concluded that the deep sea demersal fish fauna in the Sea of Japan is exclusively composed of limited numbers of species with geographical distributions typical to the Sea of Japan as shown in Table 1. It was also proved that relevant ichthyofauna is mainly composed of the secondary deep-sea fishes sensu Andriashev (1953), so that such an assemblage corresponding to "the taraba community III" sensu Nishimura (1966) can be properly referred to pseudoabyssal fauna according to Ushakov (1949).

2. Systematics and biology of main families

2.1 Rajiidae

Bathyraja smirnovi, a sole deep sea elasmobranch in the Sea of Japan, is in striking contrast with other species of this community by its larger size (>1 m TL). *Kaiyo-Maru* collections produced a total of 396 specimens (209–1050 cm TL) from 41 (95.3%) stations (Fig. 4), which were evenly distributed throughout the sea with gradual decrease toward the lower limit below a depth of 1000 m (Fig. 5). With the exception of a single trial on the North Yamato Bank (460 m), however, this fish had distinctly higher biomass in 500–1000 m than in >500 m and <1000 m deep, with the peak density around the abundance of 13–15

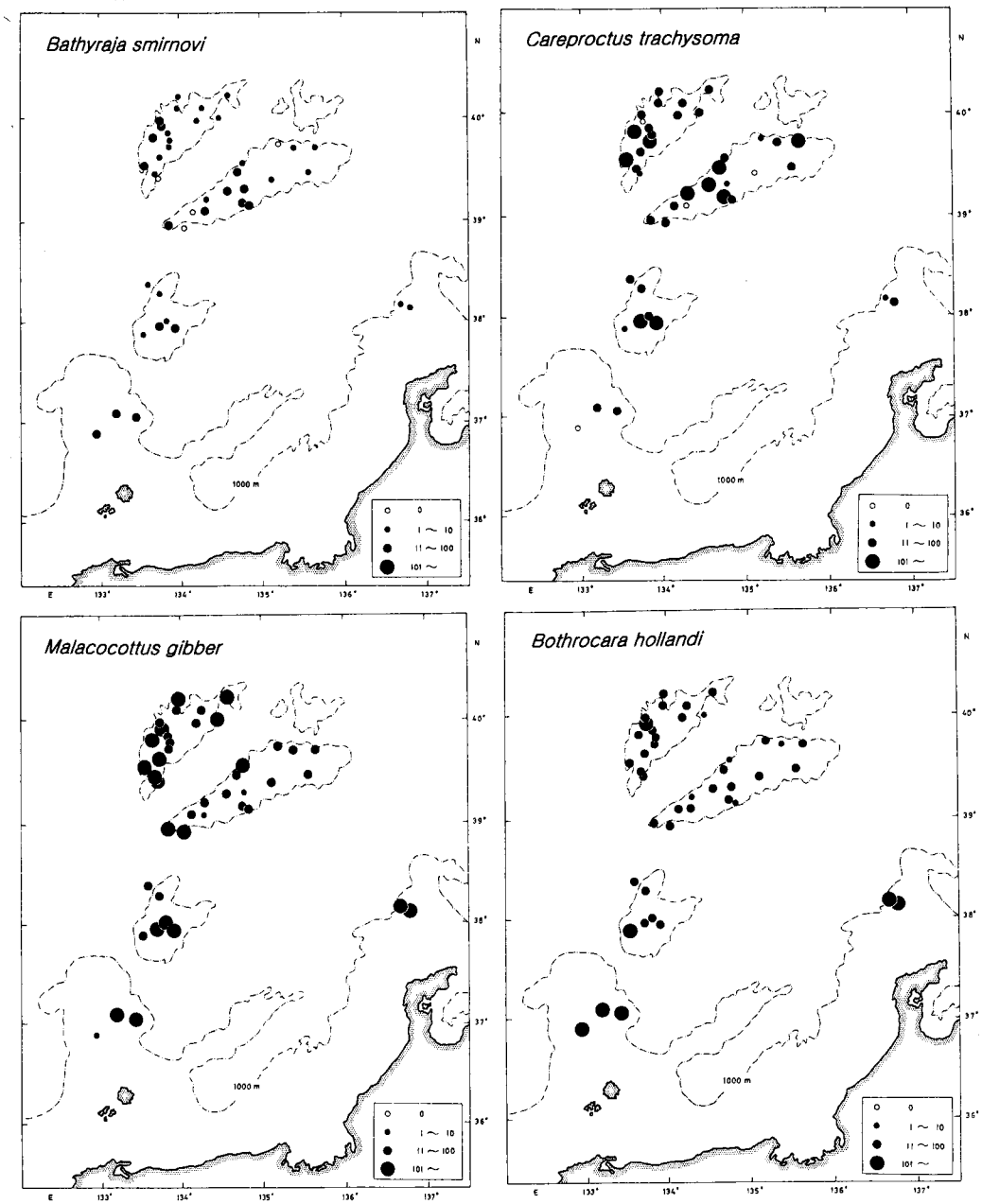

Fig. 4. Abundance and distribution of dominant four species in *Kaiyo-Maru* collections.

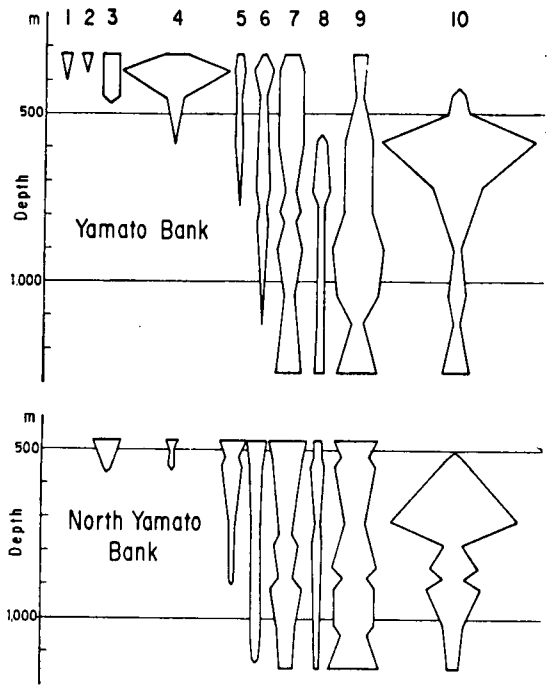

Fig. 5. Vertical profiles of relative abundances in main deep sea demersal fishes on the Yamato-Bank and North Yamato-Bank in *Kaiyo-Maru* collections: 1, *Glyptocephalus stelleri*; 2, *Hippoglossoides dubius*; 3, *Acanthopsetta nadesnyi*; 4, *Theragra chalcogramma* 5, *Arctoscopus japonicus*; 6, *Bathyraja smirnovi*; 7, *Bothrocara hollandi;* 8, *Petroschmidtia toyamensis*; 9, *Malacocottus gibber*; 10, *Careproctus trachysoma.* (Adapted from Ogata et al., 1973)

specimens (Fig. 6), probably implying a limit of carrying capacity of this top predator, at least in the summer season. There were no significant differences in sex ratio (44.9) as well as size frequencies by sex (Okiyama, 1980). Morphometric analysis of these materials (Kato, 1971) suggested two factors relating to growth and maturity, with particular concern to the male characters.

2.2 Psychrolutidae

Malacocottus gibber, a single representative of the family, is among the dominant species appeared in all stations of *Kaiyo-Maru* collections (Fig. 4). Of a total of 4458 specimens of this collection, the greatest catch amounted to 430 at station 39 on the New Oki Bank (505 m). Vertical profile of these materials did not show any particular depth-abundance relationship (Fig. 5) for the depth ranges from 255 to 1220 m. In much deeper sea, however, extremely limited numbers of individuals have been recorded until the depth of 1740 m (Table 2), implying possible depauperation of this species in these deeper zone.

There are no clear differences in size frequencies throughout its range with common peak around 13–15cm SL and sometimes another small peak in larger specimens (Fig. 7). Although possible size at first maturity (146 mm SL) lies within sizes of peak frequency, mature specimens were extremely limited in this summer collections, from which some

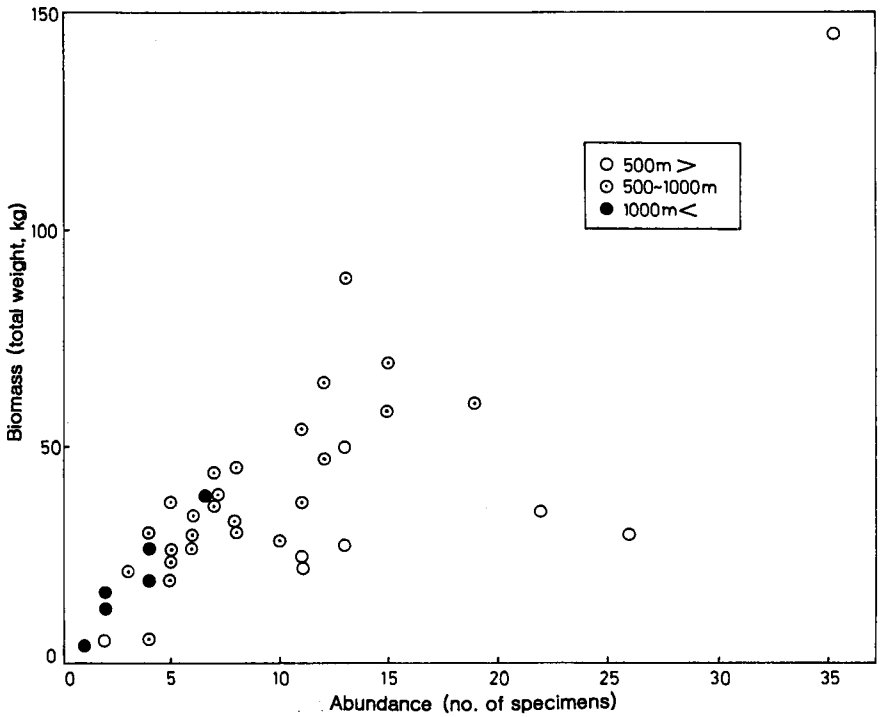

Fig. 6. Relationships between biomass and abundance of *Bathyraja smirnovi* per 30 min tow by three depth ranges in *Kaiyo-Maru* collections.

reproductive characters were obtained as shown in Table 3: Clearly, they have highest fecundity with the smallest group of eggs among the main species in this community.

Shinohara et al. (1993) first reported the mesopelagic capture of 35 adult specimens from 400–420 m deep over the soundings of 800-1500 m in the northern Sea of Japan in October. Whether seasonal or not, their pelagic occurrences as adults as well as larvae (Kojima and Okiyama, 1988) would serve to active exchanges of genes in this primarily sedentary fish.

2.3 Cyclopteridae

Aptocyclus ventricosus represents a single species of cyclopterid fauna in the depth ranges below 500 m. Since it occurred abundantly in the midwater trawls in the depths between 150 and 515 m throughout Aleutian Basin (Yoshida and Yamaguchi, 1985), its available records by means of bottom trawls have problems of contamination in discussing the vertical distribution, Supposing that a total of 21 specimens from 16 stations (37 %) in *Kaiyo-Maru* collections (Fig. 8a) were captured in the close vicinity of sea floors, they would have been distributed widely as well as sparsely (1–4 specimens per haul) on the bottom below a depth of 400 m. Its absence in shallower haul seems to supports above

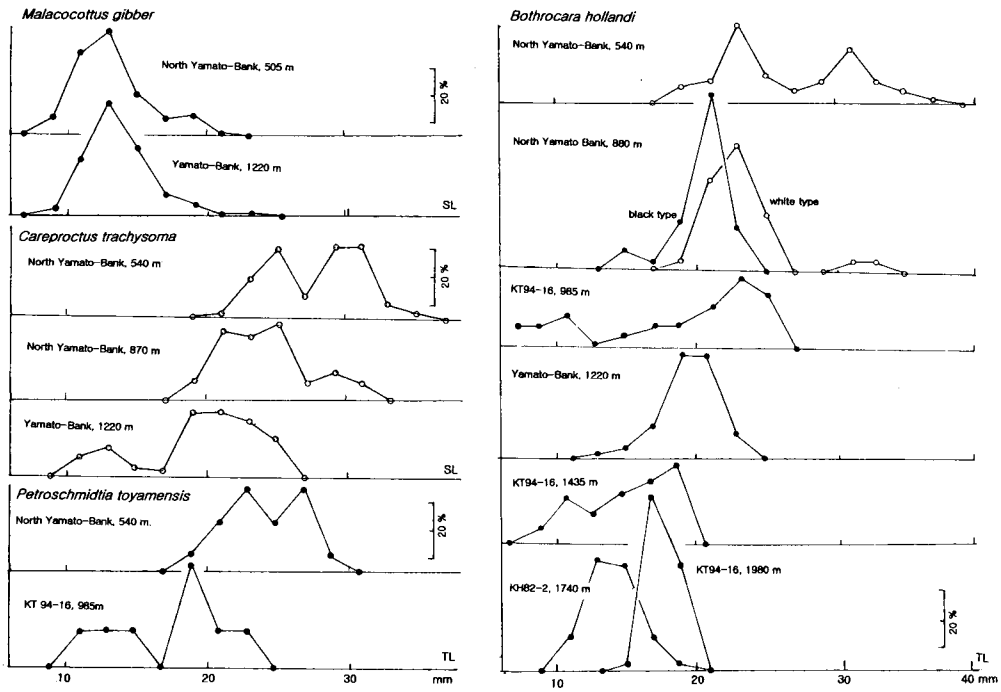

Fig. 7. Bathymetric series of size frequency distributions for main four species. In *Bothrocara hollandi* on the right side, open symbols indicate white type specimens, and closed ones black type. The right bottom figure includes frequency of deepest two collections.

assumption. Interestingly, their sizes (85–37 cm TL) are nearly the same with those (9–36 cm TL) collected by midwater trawls in the summer season in Aleutian Basin (Yoshida and Yamaguchi, 1985). In addition, as in Yoshida and Yamaguchi (1985), *Kaiyo-Maru* specimens took exclusively the comb jelly, *Beroe cucumis*, as many as 8–43 specimens per predator.

Fig. 8b was prepared based on the measurements of alive or fresh specimens on board the R/V *Kaiyo-Maru*, hoping to provide some information responsible for their peculiar feeding habits. As in tetraodontids, they swallowed a large volume of water when stimulated, so that such a behavior was expected to favor effective suction feeding on pelagic animals like ctenophores. At the same time, water volumes thus obtained and gut lengths increased similarly against body sizes (Fig. 8b), which may be adaptive to the effective use of these energy poor materials.

2.4 Liparidae

Careproctus sp. A and B in *Kaiyo-Maru* collections (Ogata et al., 1973) were proved to be *C. trachysoma* and *C. ochotensis* (Nambu and Kido, 1990; Nambu et al., 1992), respectively. *Careproctus trachysoma* was the most abundant species in the relevant

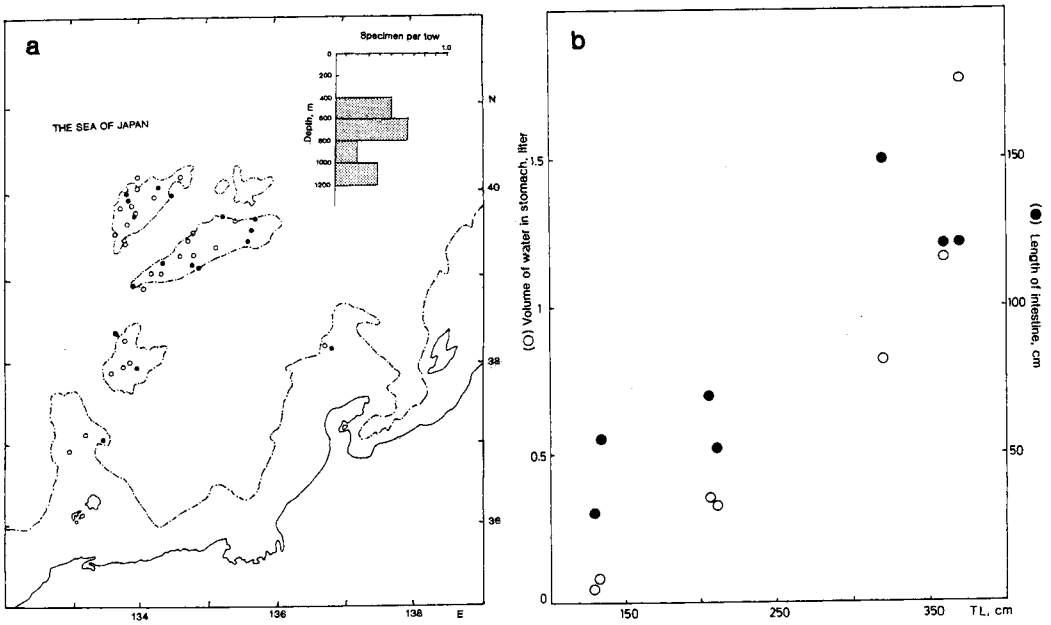

Fig. 8. (a) Distribution of *Aptocyclus ventricosus* in *Kaiyo-Maru* collections and (b) relationships between length of intestine and volume of water swallowed and body size.

collections, covering most stations except a few trials shallower than 460 m. Its distribution pattern is peculiar in that large catches tend to be concentrated on the off-shore banks (Fig. 4) with distinct peak abundance at the level of 500–800 m deep (Fig. 5). The largest catch of as many as 1845 specimens was recorded at the depth of 565 m on the Yamato-Bank having a unimodal size composition with a peak around 21–22 cm in the ranges of 18–29 cm SL. Another large catches comprising 20–35 cm specimens from 540 m on North Yamato-Bank, were composed of bimodal size groups with modes around 20–26 and 29–30 cm SL, respectively. Despite local variations, this smaller size groups dominated in catches with some deeper-smaller trend throughout most of its ranges until the depth of 1220 m (Fig. 7). It is of interest that much smaller size group less than 16 cm occurred mostly in deeper ranges of this species.

Some reproductive characters obtained from *Kaiyo-Maru* collections were given in Table 3, although mature specimens were very limited as in *M. gibber*. They have slightly high fecundity with relatively large egg size among the relevant fish fauna. Fully matured ova of a 21 cm specimen were composed of two size groups such as 4.68–5.65 mm in diameter and less than 2.19 mm.

As mentioned later, feeding habits strongly suggest possible benthopelagic life of this species. Their bodies are covered by thick gelatinous integument, probably in favor of this life style. If this is the case, qualitative estimates of this species based on the bottom trawl catches need further consideration.

Table 3. Reproductive characters of main deep sea demersal fishes in the Sea of Japan.

Species	Fecundity	Diameter of largest ova (mm)	Size at maturity (mm)	Sources**
Malacocottus gibber	2128-6630	3	146, SL	1
Careproctus trachysoma	384-1136	6.7	244, SL	1
Bothrocara hollandi	41-57*	9.2 (8.8-9.5)	194, TL	1,2
Petroschmidtia toyamensis	18-120	7.3	200, TL	1,3
Lycodes nakamurai	31-74	6.8	186, TL	1,4
Lycodes tanakae	Many	2.5	650, TL	5
Lycodes japonicus	20-23	3.5	129, TL	6

* The upper range described as 180 (Okiyama, 1982) was revised.

** 1, *Kaiyo-Maru* collections; 2, Okiyama (1982); 3, Matsubara and Iwai (1951a); 4, Katayama (1949); 5, Ishikawa Pref. Fish. Exp. St (1981); 6, Matsubara and Iwai (1951b).

Of the other two rare species of the family, *Careproctus colletti* were represented by a total of 12 specimens of similar size (30–34 cm SL) sporadically occurred at 8 stations down to 840 m deep in *Kaiyo-Maru* collections.

2.5 Zoarcidae

This family is most speciose in the relevant fauna by comprising 7 species, of which *Bothrocara hollandi* is most prosperous and occurred at all stations in *Kaiyo-Maru* cruise (Fig.4), with geographical tendency ascribed to the inshore type. Its remarkable predominance in the catches of Watanabe et al. (1958), Ishiyama and Nakamura (1968) and Ishikawa Pref. Fish. Exp. St. (1981) among others clearly illustrate this trend. In most of the previous reports, this species were described as *Allolepis hollandi,* but Anderson (1994) synonymized *Allolepis* with *Bothrocara.*

Vertical distribution of this species is remarkably eurybathial, having uniform abundance-depth relationships in the off-shore stations in *Kaiyo-Maru* collections (Fig. 5), while it was more abundant at the depths shallower than 500 m in the coastal stations (Ogata et al., 1973). Several *Tansei-Maru* collections below the depths of 1300 m (Table 2) revealed that this species clearly represents the deepest demersal fish fauna in the Sea of Japan. Although its available record does not extend beyond a depth of 2000 m, it is remarkable that this species was rather abundantly obtained near the lower reaches of its deeper bathymetric ranges.

Another interesting discovery in this connection is the presence of two morphotypes, tentatively termed as "white typ" and "black type" (Fig. 9). Strictly speaking, body coloration of the former is pale or pink, and that of the latter is dusky. Since they are readily discriminated by this contrasting coloration, most of the *Kaiyo-Maru* specimens were measured separately on board the vessel. Fig. 10 shows the depth-related tendency of their associations thus obtained, clearly showing that the white type representing shallower morphotype is replaced gradually by the black type representing deeper morphotype at depths from 700 m through 1000 m. In addition, as shown in Fig.8, two morphotypes differ

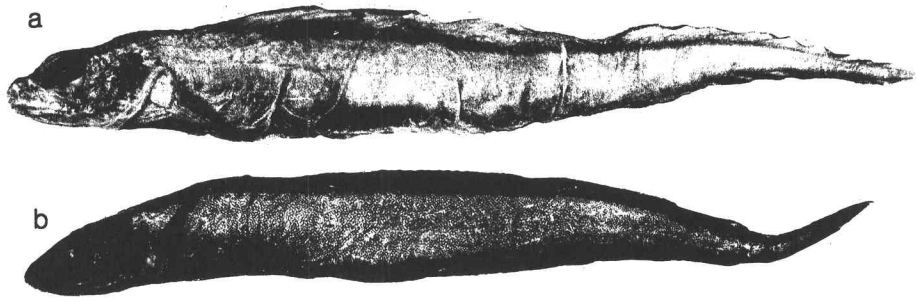

Fig. 9. Two morphotypes of *Bothrocara hollandi*: a, white type (234 mm TL); b, black type (205 mm TL).

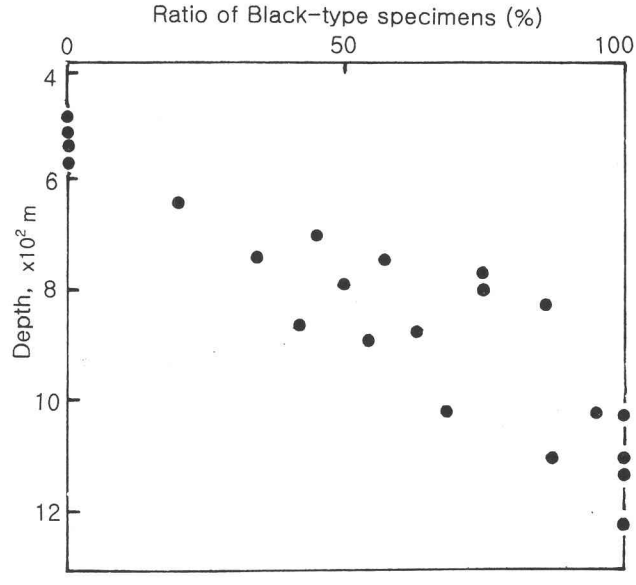

Fig.10. Depth related changes in ratio of black-type specimens of *Bothrocara hollandi* based on *Kaiyo-Maru* collections.

in body sizes, too. The black type is distinctly smaller than 26cm whereas white one grows to 36 cm TL.

Currently, evidences of their morphological (meristic) as well as genetic differentiation have not been available, although Kojima et al. (2002), having studied extensive collections from the depths of 375–1561 m in the coastal waters of the Sea of Japan, found distinct monophyletic group of haplotypes based on nucleotide sequence of

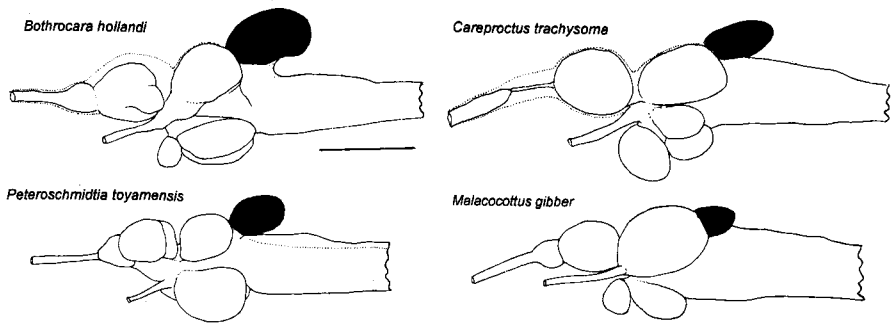

Fig. 11. Comparison of brain forms among main four species. All figures are adjusted to the same size (scale bar 5 mm) and corpus cerebelli is indicated by black.

part of the mitochondria control region, only from shallower sites less than 1000 m deep. Further molecular analysis is needed to settle taxonomic problem of these morphotypes.

Depth-related color changes are well known for the eye size and body coloration in secondary deep-sea fishes (Rass, 1966), including, for example, zoarchids of the genus *Lycenchelys* which change from a pale to dusky coloration between the depths of 90–1100 and 500–1500 m. It is of particular interest that probably analogous color change was observed within a single species of *Bothrocara hollandi* of the same family, whereas eye sizes do not alter in this case. Extremely eurybathial distribution of this species may be responsible for this phenomenon rather than specific differentiation.

Bathymetric series of length frequency distributions (Fig. 7) revealed additional depth related changes in the population structure. As mentioned before, shallower depths exclusively occupied by white type specimens were composed of polymodal size frequencies, followed by similar but more complicated compositions due to the mixture of two morphotypes in the depths from 700 to 1000 m. Limited materials from further depths exclusively composed of black type specimens clearly show a deeper-smaller trend, resulting in a unimodal size distribution with narrow ranges smaller than 19–20 cm TL at 1740–1980 m. It is of particular interest that 19–20 cm TL corresponds to the possible size at first maturity (Fig. 11, Table 3). Therefore, there is a strong likelihood that some reproductive factors are involved in determining the lower limit of its vertical distribution.

Reproductive characters of five zoarcids are compared in Table 3, and size-fecundity relationships are also given for three common species among them (Fig. 11). *B. hollandi* is conspicuous in having unusually large eggs attaining 8.8–9.5 mm in diameter which were observed in 234 mm TL specimen collected on the New Oki-Bank (570 m). They are spherical, with massive yolk in orange yellow color and large oil globule, without particular materials around the chorion.

It is very interesting that this egg size is close to the known upper limit in the teleosts (9.2–9.8 mm in diameter) found in the South-American zoarcid, *Austrolycus depressiceps* (Matallanas et al., 1990). Although both species belong to the Zoarcidae, they have remarkable contrast in habitats such as the deep sea bottom vs. the rocky intertidal level and

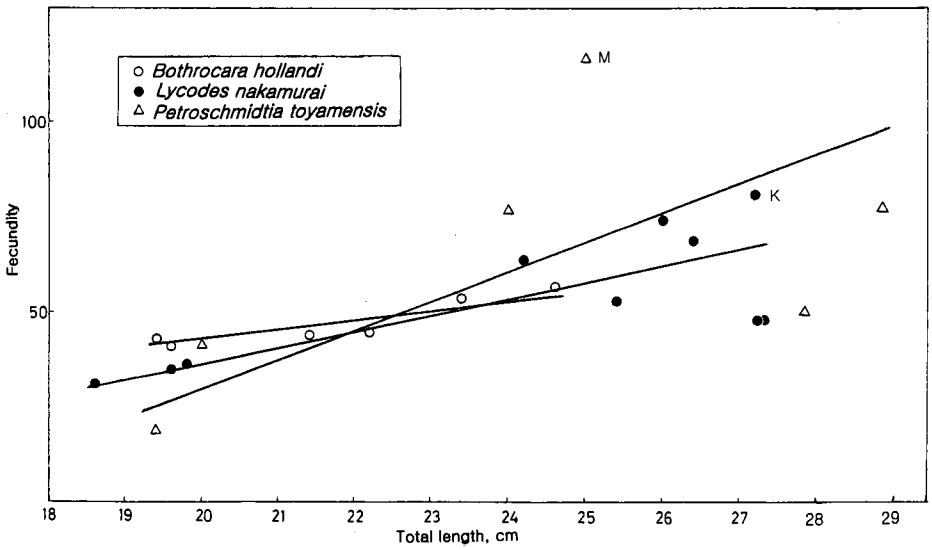

Fig. 12. Fecundity-total length relationships in three species of deep sea zoarcids based on *Kaiyo-Maru* collections, Katayama (1949) and Matsubara and Iwai (1952a). Data cited from references are indicated by the initial 'K' and 'M'.

the northern vs. southern hemispheres, in addition to the difference of fecundity like 41–57 vs. 465.

Judging from these contrasting features, it is likely that their exceptionally large eggs have developed independently along a suggested trend such as "high latitude and deep-sea fishes have fewer and larger eggs" (Marshall 1953) with systematic restriction of this group.

No information is available for the eggs of *B. hollandi* in the field. Kendall et al. (1983), however, hypothesized that *Bothrocara* sp. (?) obtained from a depth of 1265 m off Washington State deposited eggs (7 mm mean diameter, fecundity ca 27) into the bottom sediments as deep as 10 cm. If such is true of *B. hollandi*, complete lack of relevant information in this species is quite natural. Large newly hatched larvae reflecting a large investment (4 specimens; 34–36 mm TL) were obtained from the stomach contents of *Lycoides tanakai*, and 35.5 mm specimen was first described (Okiyama, 1982).

There is an interesting chemical analysis of three common zoarcids, revealing distinctly higher water contents (89–90 %) in *B. hollandi* than in *Petroschmidtia toyamensis* and *Lycodes tanakai* (80–82 %) (Ishikawa Pref. Fish. Exp. St. 1981). Such a feature surely give significant benefits to *B. hollandi* by providing lower specific gravity, thus causing more active movement by smaller energy expenditures. This assumption may be supported by a specialization of the brain form (Fig. 10), since *B. hollandi* has well developed corpus cerebelli suggestive of higher activity and more enhanced sense of the equilibrium (Ito and Yoshimoto, 1991) as compared with those of other common species including *P. toyamensis*. Likewise, relatively larger corpus cerebelli in *Careproctus trachysoma* may be associated with its benthopelagic lifestyle as mentioned before.

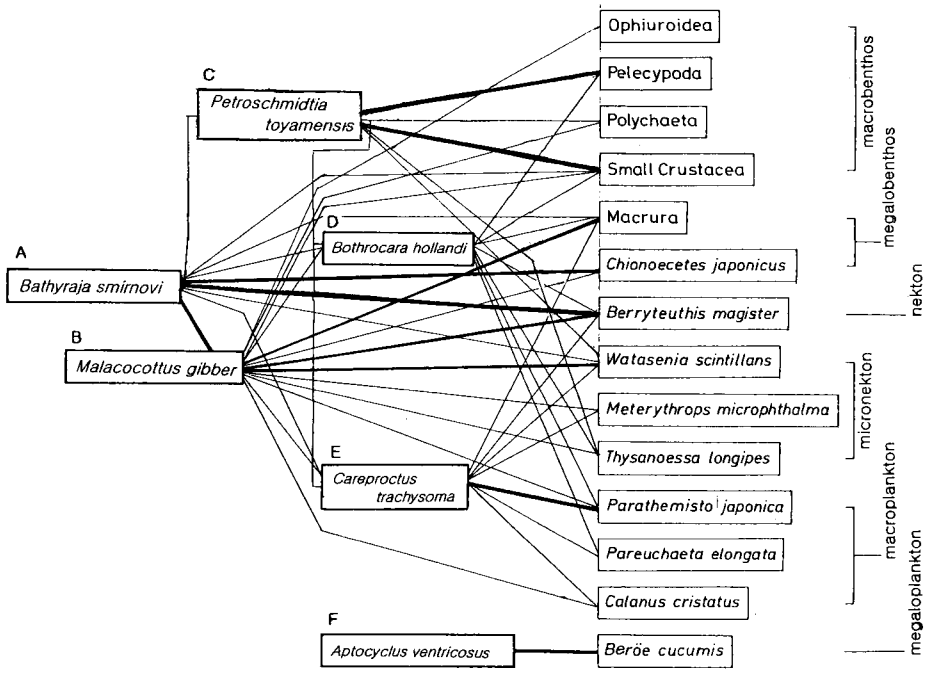

Fig. 13. Food web interactions among main fishes in the deep sea community of the Sea of Japan. Alphabet attached to species name indicates feeding type.

Petroschmidtia toyamensis is among the deepest four species in the sea with lowest limit at depth of 1429–1437 m (Table 2), and the second most abundant zoarcids in *Kaiyo-Maru* collections. It was referred to the universal type of distribution having unclear depth-abundance relationships (Fig. 5), while deeper-smaller tendency is also distinct in this species (Fig. 7). Its reproductive characters (Table 3; Fig. 12) are very similar to those of *B. hollandi* except for slightly smaller egg associated with more variable fecundities, steeper slope in fecundity-size relationship and larger size limit of reproductive activity.

Other zoarcids are either common or rare elements restricted to the depths less than 1000 m, of which *Lycodes tanakai* is conspicuous in its exceptionally large size (20–80 cm TL) and higher fecundity (Table 3), as well as restriction to the inshore stations of *Kaiyo-Maru* collections. Interestingly, these zoarcids except *L. tanakai* have similar reproductive characters such as small sizes at first maturity, very low fecundity with a similar increase dependent on body size (Fig. 12) and moderately or extremely large eggs (Table 3), although there are slight differences among them in some aspects such as the upper limit of reproductive sizes and the slopes of linear fecundity-total length relationships. Such a reproductive strategy seems common to this group (Merrett and Haedrich, 1997).

2.6 Pleuronectidae

All four species included here belong to the same zoogeographical group comprising temperate and boreal elements chiefly distributed in narrow areas such as the Sea of Japan

and adjacent seas (Moiseev, 1953). Although most of their deeper records are very limited and barely extend beyond 500 m deep, recent study revealed common occurrences of *Hippoglossoides dubius* in this deeper part down to 720 m during summer season (Hirose and Minami, 2003). If this is a regular event, we must take seasonal patterns of vertical migrations into consideration even in these deep sea under constant temperature conditions throughout the year.

Table 4. Compositions of stomach contents in terms of percentage of major groups by frequency method. Figures in parentheses are cited from Watanabe at al (1958).

Species	Plankton	Benthos	Nekton	Main prey species
Bathyraja smirnovi	1.8	40.3	57.9	*Barryteuthis magister* *Chionoecetes japonicus*
Malacocottus gibber	16.2 (38.8)	37.9 (34.7)	55.9 (26.5)	*Barryteuthis magister* *Watasenia scintillans*
Aptocyclus ventricosus	100			*Beroe cucumis*
Careproctus trachysoma	95	1.5	3.5	*Parathemisto japonica*
Bothrocara hollandi	40.7 (81.3)	35.8 (13.3)	23.5 (5.4)	*Parathemisto japonica*
Petroschmidtia toyamensis	12.8 (5.0)	73.0 (93.5)	14.2 (1.5)	*Yoldiella philippiana* *Nucula palua*
Lycodes nakamurai	19.5 (21.0)	41.3 (75.4)	39.1 (3.6)	*Watasenia scintillans*

3. Feeding habits and food web interactions

Chiefly based on *Kaiyo-Maru* collections, feeding habits of common fishes were analyzed in terms of percentage of major prey groups by frequency method. Results were summarized in Table 4, where some relevant figures were included from Watanabe et al. (1958). Disparity in several figures may be due to either segregation of localities surveyed, or different definition of some prey categories. By taking size and life forms of main food items into consideration, these fishes were roughly divided into six types of feeding groups as follows:

A. Megalobenthos and nekton feeder – *Bathyraja smirnovi*
B. Megalobenthos, macrobenthos and micronekton feeder – *Malacocottus gibber* (*V*)
C. Macrobenthos and micronekton feeder – *Petroschmidtia toyamensis* (*Q*), *Lycodes nakamurai* (*R*)
D. Macrobenthos and macroplankton feeder – *Bothrocara hollandi* (*S*)
E. Macroplankton feeder – *Careproctus trachysoma*
F. Megaloplankton feeder – *Aptocyclus ventricosus*

Alphabet in parenthesis behind each species indicates the type of feeding habits in Watanabe et al. (1958).

It is remarkable that most of these types are represented by a single species. Except for the last two groups devoting to particular pelagic prey animals such as *Parathemisto japonica* (amphipod) in type E and *Beroe cucumis* (ctenophore) in type F, food compositions in other types were variable, particularly in types B and C. In this connection, an interesting prey partition was observed between two species of type C at St. 10 on the

Yamato Bank (565 m): *P. toyamensis* exclusively took ophiuroids along with a few other macrobethos, whereas *L. nakamurai* mainly fed on the micronekton such as *Watasenia scintillans* and *Thysanoessa longipes*. Apparently, their prey selection corresponds to the difference between types *Q* and *R* in Watanabe et al. (1958), but such a division was obscure as a whole in *Kaiyo-Maru* collections.

Berryteuthis magister, the dominant prey of types A and B, has peak concentration in the upper 300 to 500 m and rapidly decreases downward until around 1200 m (Okiyama, 1993). Similarly, several micronectonic invertebrates such as *Watasenia scintillans*, *Metherythrops microphthalma*, and *Thysanoessa longipes*, which are important preys of types B and C among others, are known to inhabit mainly the midwater depth shallower than 1000–1500 m or less, as in *Parathemisto japonica* concentrated above 1000–1500 m (Sazhin and Vinogradov, 1979). All these features indicate that abundance of major prey organisms becomes very poor in the deep sea below 1000–1200 m.

In contrast, *Chionoecetes japonicus*, important prey species of types A and B, reportedly penetrates into 2500 m or more (Nishimura, 1966), while its availability is indistinct below the depth of 1000–1200 m.

Empty stomachs were generally frequent in types C and D, especially in *B. hollandi* depending on stations. On the other hand, prey-predator relationships between fishes were common between *B. hollandi* and other species of types A, B and C. Perhaps, such interactions are more conspicuous in the coastal regions having additional predators such as *Hippoglossoides dubius*, *Acanthopsetta nadesynii* and *Lycodes tanakae*.

Based on these limited materials in particular seasons, possible food web interactions among main fishes chiefly in the ranges of 500–1000 m deep were outlined in Fig. 13, where connections by thick lines indicate skeletal interactions with frequency exceeding 30 % of fed specimens

From this figure, it can be said that deep-sea demersal fish community in the Sea of Japan is provided with a typical pattern of trophic interactions, despite extremely poor fauna. Effective partition of food resources seems also established among species in this community. However, its web stability associated with species richness may decrease below the depths of about 1000 m, through a gradual dropping out of type A and F, followed by C and E, then B until the deepest D. It is also likely that, in general, nektonic and/or planktonic organisms play very important role in food-web of this community as compared with benthic prey, emphasizing the importance of active transport of nutrition from upper layers by pelagic animals in this sea. In this connection, it is conspicuous that *A. ventricosus* of type F depending solely on *Beroe cucumis* does not share any interactions with other members of this community. Its unique life style including peculiar feeding habit would be of great advantage for this cyclopterid to exploit the broad vacant niche in this sea as in the Aleutian waters (Yoshida and Yamaguchi, 1983).

Finally, it should be emphasized that *B. hollandi* of type D plays the most important role in the economy of this deep sea demersal fish community by variously intervening in the relevant trophic interactions. Its feeding habit depending stronger on pelagic prey, however, may be a critical facet in extending the lower limit of its eurybathial distribution.

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